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TYPES OF
CLAYTONIA GRONOV

BY

THEODOR HOLM

SÆRTRYK AF
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In the early spring, long before the willows and birches have brought forth their catkins, but contemporarily with *Erigenia* and *Anemone*, the beautiful flowers of *Claytonia* greet us when wandering through the woods and glades; "Spring-beauty" is the popular name of this plant. All along the Pacific coast, from Alaska to California, *Claytonia* abounds in forests, about springs and along streams. In the Rocky Mountains, in the Aspen-zone, in the dark, shady swamps beneath the alders, where the beaver has its home, the dainty, little *Claytonia Chamissonis* covers the black soil with its snow-white flowers. And on the lofty summits of these mountains, amidst the bowlderfields, *Claytonia megarrhiza* thrives and adorns the rocks with its beautiful flowers and rich verdure. Truly alpine as it is *Claytonia megarrhiza* may have witnessed the epoch, known as the glacial, when arctic and alpine flowers met: when *Dryas*, *Cassiope*, the polar willows, the birches, the arctic *Saxifragas*, *Silene*, *Diapensia* and *Rhodiola* were driven south, and sought refuge on these peaks; some to remain and persist, others to succumb.

Westward to the mountains of Altai, famous as being the home of so many arctic plants, we find *Claytonia* represented by several species. Finally, and so very remote from its natural boundaries, *Claytonia* appears in Australia and New Zealand with a few species, truly endemic. In recent time there is no species of *Claytonia* in the arctic region, and the genus is evidently of North American origin, unless the East-Asiatic element: *Cl. tuberosa*, *arctica* and *sarmentosa* be of arctic origin.

By no means uniform in structure *Claytonia*, nevertheless, has preserved several characteristics of its own wherever it has spread. From the lowlands of the warm temperate zone to the alpine regions, and to near the arctic circle the genus shows unmistakebly the same principal features in respect to the floral structure, while the vegetative equipment is quite distinct; annual or perennial as the species may be, they always are readily recognized as being members of the genus. In considering the fact that *Claytonia* does not contain more than about thirty species, it is surprising to notice that no less than five, very distinct, sections are necessary to combine these with each other in a systematic manner; however the distinctions depend mainly on purely vegetative characters.

To Asa Gray[1]) we are indebted for the first and most logical outlining of the genus,

[1]) Proceed. American Acad. Boston 1887, p. 278.

establishing five sections viz. *Euclaytonia*, *Limnia*, *Alsinastrum*, *Naiocrene* and *Montiastrum*. Characteristic of *Euclaytonia* is the relatively large, primary, persisting root; in *Limnia* the roots are fibrous, and the species mostly annual. Then in *Alsinastrum* we have the peculiar *Cl. Chamissonis* with all the leaves opposite, and with bulbiferous stolons; in *Naiocrene* which is, also, perennial, bulblets are developed in the axils of many of the cauline leaves. Finally in *Montiastrum* the species are strictly annual with mostly alternate leaves, and with mostly two of the stamens suppressed. In other words several of the species are annual, and among those which are perennial we meet with some that possess large persisting roots, and others in which these are fibrous and fugacious, but where the vegetative reproduction is secured by means of bulblets, aerial or subterranean.

Now in respect to the structure of the shoot, we have shown[1]) that the inflorescence is frequently lateral, and indeed most frequently so. The inflorescence is of the cymose type, but the lateral ramifications are frequently monochasia of the type cicinnus or scorpioid cyme, as described by Wydler[2]). Preceding the inflorescence we frequently notice one pair of opposite leaves, which by Eichler and Wydler have been defined as prophylla; the flowers themselves are mostly destitute of such foreleaves, but there are some species, however, in which one of these is developed, especially in the lower part of the inflorescence. Most frequently the two foreleaves, preceding the inflorescence, are the only leaves of the aerial stems, but in some few species, as will be shown later, the stems are leafy from the base to the inflorescence, opposite in *Cl. Chamissonis*, alternate in *Cl. linearis* and *parvifolia*.

In outlining the genus Gray (l. c.) did not distinguish between species with the shoot terminated by an inflorescence or being purely vegetative, nor did he consider the character "annual" or "perennial" of much importance to his classification. Nevertheless in all the members of *Montiastrum* the shoot is terminated by an inflorescence, but not so in any of those of *Limnia*. The duration of life of these species, annual or perennial, does not seem to be of any importance, inasmuch as we know that annuals sometimes become perennial, and in *Claytonia* this is illustrated by *Cl. Sibirica* according to Gray (l. c.).

Let us now examine the types of the genus, classified as suggested by Gray, and considered inseparable from the genus *Claytonia*.

Euclaytonia.

Claytonia megarrhiza Parry (Plate I figs. 1—15).

Undoubtedly the most remarkable of the genus. A seedling has been figured on Plate 3 fig. 1, and we notice the distinct primary root, the short hypocotyl, and the two

[1]) Memoirs U. S. National Acad. of sc. Washington 1905, p. 29.
[2]) Flora 1851, p. 348.

cotyledons above ground; at this stage two leaves, succeeding the cotyledons, are already visible, and the plant is now ready to meet the first winter. During the winter the hypocotyl shows a gradual wrinkling, by which the plumule becomes pulled down beneath the surface of the ground, and the root continues its growth vertically, and to a very considerable depth. In the following spring several leaves develop and form soon a small rosette, while increase in thickness commences in the hypocotyl and in the basal portion of the root. A fully matured specimen is figured on Plate 1, showing the large root, the rosette of leaves, and the inflorescences, all axillary. In this illustration we have before us the picture of a plant that inhabits the highest peaks of the Rocky Mountains. And at the stage figured the leaves and inflorescences for the coming year are already developed, and visible when we lay a longitudinal section through the rosette and the apical portion of the hypocotyl. The leaves vary from spatulate to dilated-cuneate or obovate (figs. 3—5); the inflorescence (fig. 2) is cymose with the two large foreleaves empty, and with only one bract to each cyme. In respect to the structure of the flower (figs. 6 and 8) this agrees with *Claytonia* proper; so does also the opening of the capsule (figs. 9—14), and the seed (fig. 15).

If we compare this species of *Claytonia* with the other high alpine plants of the Rocky Mountains, the deep-seated root seems somewhat anomalous; but otherwise the leaf-structure, for instance, is that of many alpine species, this being isolateral, the stomata being distributed over both faces of the blade, and the chlorenchyma representing a palisade-tissue throughout.

A similar development of the root and foliage exists in *C. arctica* ADAMS and *C. tuberosa* PALL., but not in the other species pertaining to this section.

Claytonia Virginica L. (Plate II fig. 1).

This is, also, a relatively large-rooted species, in which the primary root increases considerably in thickness, but only the basal portion, since the slender apical part dies off entirely. In respect to the seedling-stage we find only one cotyledon developed, hence reminding of *Ficaria*, *Cyclamen*, *Dicentra* etc. The ramification of the shoot is monopodial, but the leaves do not persist throughout the winter as is the case with *C. megarrhiza* PARRY. In regard to the leaf-structure this is dorsiventral so far as concerns the chlorenchyma, but not in respect to the stomata, which occur on both faces of the blade. *Claytonia Caroliniana* MICHX. and *C. lanceolata* PURSH agree with *C. Virginica* L.

Claytonia sarmentosa C. A. MEY.

The last member of *Euclaytonia*, since we prefer to place *C. asarifolia* BONG. under the section *Limnia*. In *C. sarmentosa* C. A. MEY. (Plate II fig. 2) we notice the deep

root, which is slender, and ramified. There is an overwintering rosette of leaves, and the shoot is monopodial as in the species described above. But a notable difference exists in the production of stolons, which are above ground, and which consist of one long internode. In this way the species is better equipped, so far as concerns the vegetative reproduction, than any of the others of this section. The leaf-structure is dorsiventral with a very open pneumatic tissue, thus illustrating a plant well adapted to an atmosphere charged with excessive moisture, the conditions under which this species is able to thrive.

Euclaytonia thus contains species of a somewhat different habit, and of a relatively distinct anatomical structure. However characteristic of all these species is the large development of the root, the monopodial ramification of the shoot, and the simple composition of the inflorescence, provided with two large foreleaves.

Limnia.

Before the publication of "Species plantarum" Linnaeus had *Claytonia Sibirica* under the genus *Limnia;* but since then it was referred to *Claytonia* together with *Cl. Virginica.*

Claytonia asarifolia Bong.

This species is perennial by a horizontally creeping rhizome, and the ramification is monopodial, the apex of the shoot being vegetative. The two prophylla are large, but the inflorescence is simple, mostly a monochasium, and with no bracts to the flowers.

Claytonia Sibirica L. (Plate III fig. 1).

This resembles the preceding species very much, but it is mostly annual; however a perennial form does occur, and at this stage stolons become developed. In respect to the inflorescence this is generally very rich-flowered, beginning with a true cyme, the lateral branches of which may continue as cymes or pass gradually into monochasia; the floral bracts are nearly always developed. An interesting form has been described by W. N. Suksdorf[1]) as *Cl. Washingtoniana*, which is a small, delicate, annual plant with only a few flowers.

Of the same habit, but strictly annual are *Cl. arenicola* Henders., *Cl. perfoliata* Don., *Cl. parviflora* Dougl., and the very narrow-leaved *Cl. gypsophiloides* Fisch. et Mey., and *Cl. spathulata* Dougl. In the two last species the flowers are usually destitute of bracts, except the central. Characteristic of the section *Limnia* is, thus, the very broad prophylla, and the slender roots of short duration.

[1]) Deutsch. Botan. Monatsschr. 1898, p. 220.

Alsinastrum.

Claytonia Chamissonis ESCH. (Plate II fig. 3).

From all the other species of *Claytonia* this is very distinct by the stem-leaves being opposite, and by producing stolons; from those described above *Cl. Chamissonis* shows a marked difference by the stem-internodes being stretched, and by the aerial stem being branched; these lateral branches are sometimes purely floral, or they develop several pairs of opposite leaves before the flowers appear. In this species the primary axis, as well as the lateral, becomes terminated by an inflorescence, of which the fore-leaves are generally of very unequal size, the one subtending the lateral, floral branch being frequently a mere scale. The inflorescence is sometimes an ample cyme with the central flower very distinct, and with two lateral cymes passing into monochasia, but in no case have we observed the fore-leaves so distinctly represented as in the members of *Euclaytonia* and *Limnia*. Now in respect to the stolons these develop from the axils of the cotyledons already, or from the axils of the lower stem-leaves in specimens as the one figured (Plate II fig. 3) which has developed from a bulb; this figure shows the stolons consisting of slender, stretched internodes with small, opposite, scale-like leaves, and either terminated by a pointed bud or by a bulb with fleshy leaves; in this specimen the root-system is poorly represented, being reduced to some few secondary roots from the mother-bulb. In the seedling the primary root is quite long, but very slender, and does not persist; the cotyledons are epigeic.

Some few points may be mentioned in regard to the internal structure viz.: the stolons do not increase in thickness, but they contain deposits of starch in the cortex, and endodermis is slightly thickwalled. The leaves possess stomata on both faces of the blade, although the chlorenchyma shows a typical, dorsiventral structure; neither collenchyma nor stereome was observed in the leaf, and the mestome-strands are only surrounded by thinwalled parenchyma-sheaths, deeply embedded in the chlorenchyma.

Naiocrene.

Claytonia parvifolia MOC. (Plate II fig. 4).

A perennial plant with the habit very different from that of the species of the other sections. The primary shoot is erect, but very short, and terminated by a rosette of leaves; filiform, secondary roots push out from the short, subterranean internodes; the flower-bearing stems are simple, very slender, ascending or frequently procumbent, and they are lateral, being developed in the axils of the leaves. Furthermore, very characteristic of the plant is the alternate position of the cauline leaves, and the development of small bulblets in the axils of several of these; these bulblets are deciduous, and able

to develop new individuals. The inflorescence has two minute, scalelike fore-leaves, and only a few flowers arranged in a monochasium.

An extreme form is Bongard's *Cl. flagellaris* in which the weak stems attain quite a considerable length, being prostrate and runner-like.

Montiastrum.

Claytonia diffusa Nutt. (Plate III fig. 3).

At first erect, the weak stems soon become diffuse. It is an annual with a very thin primary root, crowned by a rosette of leaves, and the primary stem is terminated by an inflorescence. Characteristic of the species is the presence of several alternate leaves upon the stem from base to where the inflorescence begins, and these have long petioles, and a broad ovate blade. Only one fore-leaf is developed, and this shows the same shape as the cauline; the inflorescence itself is a monochasium. Similar to *Cl. Chamissonis* the cauline leaves subtend branches with leaves and flowers, and the plant reminds somewhat of *Stellaria media.*

Claytonia linearis Dougl. (Plate III fig. 4).

In this plant the leaves are narrowly linear; the inflorescence has only one fore-leaf, which represents a mere sheath without blade; of the stamens mostly the two are suppressed, and the petals are obviously unequal. The habit, however, is the same as that of *Cl. diffusa.*

Claytonia dichotoma Nutt. and *Cl. Howellii* (Wats.) belong to this section; they, especially the latter, are very small plants of the habit of *Cl. linearis*, but more branched, and with a larger number of flowers.

In *Cl. Australasica* J. Hooker[1]) which much resembles small forms of *Cl. linearis* the procumbent stems are rooting at the nodes, and the petals are equal; otherwise this plant agrees well with the section *Montiastrum.* But in respect to *Cl. calycina* Colenso[2]) of which the writer has seen no specimens, this seems somewhat anomalous in this section since it is said to have only two stigmata.

In bringing these data together it is readily to be seen that the vegetative characters are very pronounced, and sufficient for the establishment of the sections proposed by Gray (l. c.). That some variation in the floral structure does occur we have seen from some of the species of the section *Montiastrum*, in which the petals are unequal, and some of the stamens suppressed; however to separate these species from *Claytonia* would hardly be natural, inasmuch as no other deviations have been observed neither in regard to the structure of the calyx, the pistil or the seeds.

[1]) Icones plantarum. Vol. 3. London 1840. Tab. 293.
[2]) Transacts. and proceed. New Zealand Inst. 1895, p. 592.

It is interesting to notice the uniform structure of the inflorescence, always cymose, but more or less modified into monochasia. Furthermore the constant presence of at least one of the two prophylla; in *Montiastrum* there is but one; in *Naiocrene* both are developed, but of very minute size; in *Alsinastrum* both are present, but of very unequal size; finally in *Limnia* and *Euclaytonia* both are of the same size, and large. In regard to the stem above ground this may be leafy, or destitute of leaves except the prophylla. When only one internode is developed as in *Euclaytonia* and *Limnia* the prophylla are the only leaves of the stem, the foliage proper being borne on the extremely short central shoot; in these two sections the ramification of the shoot is monopodial, the flower-bearing stems being developed from the axils of these leaves. A like monopodium exists in *Naiocrene*, even though the flower.bearing stems consist of many internodes with alternate, green leaves. In *Alsinastrum*, on the other hand, the leafy stem is terminated by an inflorescence, and the leaves are opposite. Finally in *Montiastrum* the primary shoot is leafy from base to apex, but is not a monopodium.

The method of vegetative reproduction, also, deserves notice; bulblets sessile in the axils of the cauline leaves we have seen in *Naiocrene;* bulbiferous, subterranean stolons occur in *Alsinastrum;* stolons, subterranean, but not bulbiferous, occur, also, in *Alsinastrum*, furthermore in *Limnia*, but only in a certain form of *Cl. Sibirica;* finally in *Cl. sarmentosa* stolons above ground are well represented, and from these leafy rosettes become developed. In the large-rooted species of *Euclaytonia* the monopodial shoot winters over with a rosette of leaves in the axils of which the young inflorescences are hidden until the coming of the spring; in *Cl. Virginica* and its nearest allies with a globular, tuberous root, no leaves are visible during the winter, these being kept in the ground together with the young inflorescences, which appear before the leaves. Nearly all the species of the section *Limnia* are annual, but we have seen that *Cl. asarifolia* is perennial, and that *Cl. Sibirica*, though typically an annual, does occur as a perennial under favorable conditions. All the species of *Montiastrum* are annual. In regard to the root-system we have seen the enormous development of the primary root in *Cl. megarrhiza*, partly also in the other members of *Euclaytonia.* But in the other species the primary root is slender, and does not persist for more than one season except in *Cl. Sibirica* when perennial, and in *Cl. parvifolia*, where it, however, becomes replaced by secondary roots. Secondary roots occur, also, in *Alsinastrum*, developed from the internodes of the bulb, and sometimes also from the nodes of the slender stolons; in *Cl. sarmentosa* such roots were noticed upon the stolons, beside at the base of the leafy rosette; finally in *Cl. Australasica* the stems root freely at the nodes.

If we now compare the geographical distribution of these species of *Claytonia*, we notice the occurrence of the large-rooted *Cl. tuberosa* and *Cl. arctica* in Siberia, of *Cl. sarmentosa*, *Cl. asarifolia* and *Cl. Sibirica* on the islands of Bering Sea, from where they

extend to Alaska and adjacent islands. Of these *Cl. asarifolia* and *Cl. Sibirica* have their widest area of distribution in the Rocky Mountain Region from British Columbia to California, together with *Cl. megarrhiza*, *Cl. lanceolata*, the remaining species of *Limnia*, *Alsinastrum*, *Naiocrene* and *Montiastrum* except the Australian. On the Atlantic slope *Cl. Virginica* and *Cl. Caroliniana* are distributed from Nova Scotia to North Carolina, westward to Saskatchewan and Minnesota. The present distribution does point toward the Rocky Mountains as being an important center of development of the genus *Claytonia;* on the other hand the occurrence of such alpine types as *Cl. arctica* and *Cl. tuberosa* in the mountains of Siberia, may indicate another, and much older center of distribution. Close to the arctic circle we find some of these large-rooted *Euclaytonias*, and confined to the highest peaks: *Cl. megarrhiza.* In other words the very species that illustrate the structure of arctic-alpine types are those of which the geographical range is the widest: Altai, Alaska and Rocky Mountains.

Considered from a morphological point of view these various species of *Claytonia* exhibit several interesting types in which, however, the floral structure is very uniform and almost constant, at least in the most essential points. The vegetative structures are, on the other hand, distinct, and indeed very pronounced in some sections. Some correlation between structure and environment may be sought among those that exist under extreme conditions, and the large-rooted species of *Euclaytonia* do exhibit certain characters in common with certain arctic and alpine types, viz. the deep root, the succulent foliage, and low stature. The broad-leaved *Cl. asarifolia* and *Cl. Sibirica* illustrate the sylvan type; the peculiar, very slender, bulbiferous *Cl. parvifolia* and *Cl. flagellaris* resemble, in respect to habit, several other plants which inhabit moist rocks; in *Cl. Chamissonis* we have the structure of a number of bog-plants. But in respect to *Cl. Virginica* and *Cl. Caroliniana* so very abundant in the woods, and blooming so very early, the structure of these is rather unlike that of sylvan types in general viz. the deep-seated root, and the succulent stems and foliage; they are, however, readily referable to the genus, but they, certainly, are very distinct from the sylvan *Cl. asarifolia* and *Cl. Sibirica.*

We have, thus, in *Claytonia* a genus before us in which a number of structural peculiarities are preserved wherever the species occur. As divided into sections the members of the genus are classified in a very natural manner, and the distinctions are readily perceived; the sequence, however, is not indicated. Owing to the wide gap in geographical distribution of certain species, it is very difficult to offer a demonstration of the affinities from an evolutionary point of view. We wish we were in the position to define the groups and the species in the same clear, instructive manner as Salomon Drejer treated the genus *Carex*[1]) with *formae hebetatae*, *centrales* and *desciscentes.* In *Claytonia*

[1]) Symbolae Caricologicae. Kjøbenhavn 1844.

we are not aware of any *formae hebetatae;* as regards the *centrales* we presume these being represented by the alpine, and high northern types, but the difficulty arises when making an attempt to combine with these the perennial *Limnia*-species, *Naiocrene* and *Alsinastrum.* Furthermore it seems doubtful whether the dwarfed annuals be regarded as *formae desciscentes.* Therefore in venturing to present the following outlining of the species, we wish this to be considered as a mere suggestion.

Claytonia.

Centrales { *arctica*, *tuberosa*
megarrhiza, *sarmentosa*, *Virginica*, *Caroliniana*,
lanceolata
asarifolia, *Sibirica*
the annual species of *Limnia*

Desciscentes { *Naiocrene*, *Alsinastrum*
Montiastrum.

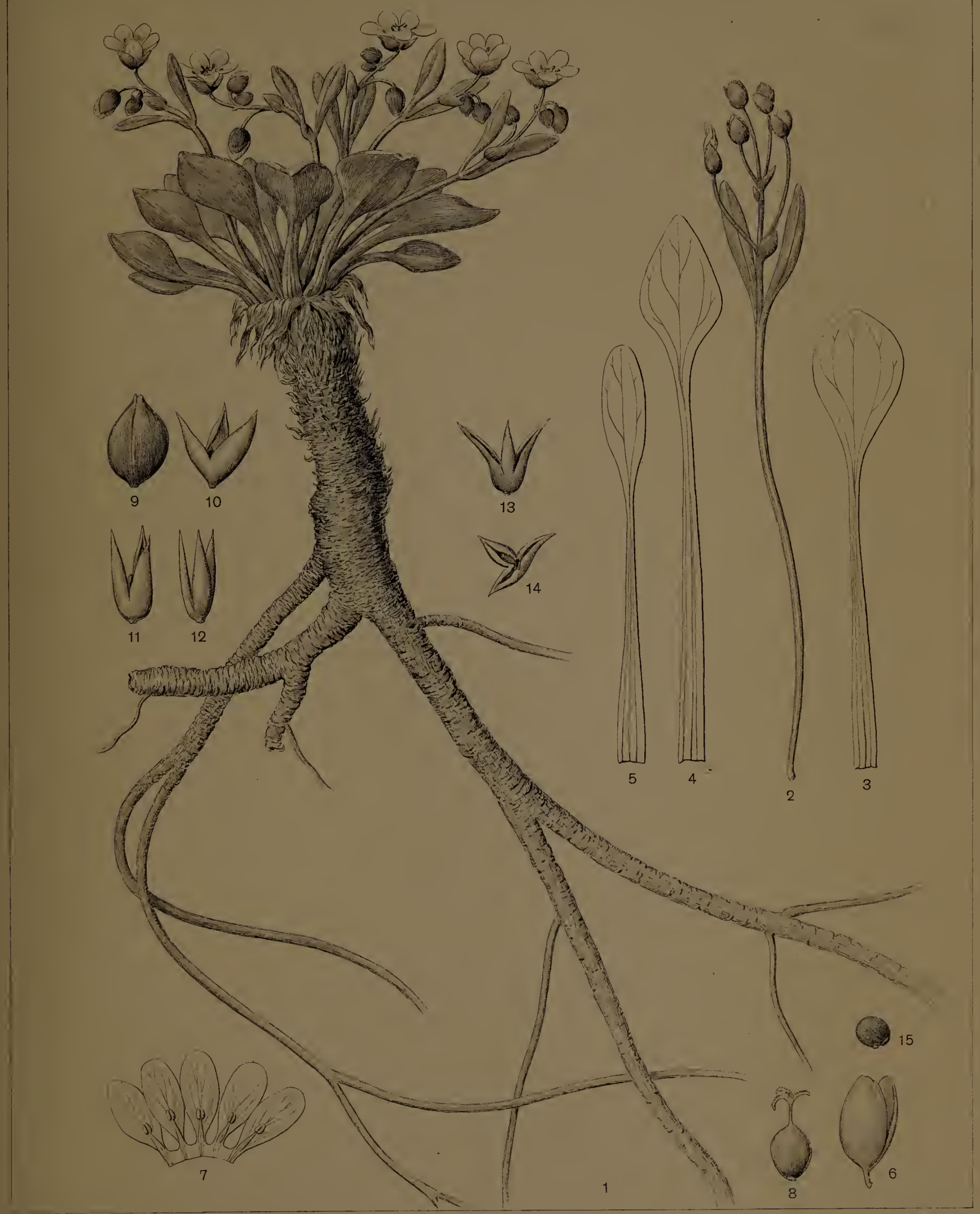
Thus we regard as fundamental species the high northern *arctica* and *tuberosa*, represented also in the mountains of Altai; parallel with these may have been *megarrhiza* and *sarmentosa*, and then: *Virginica*, *Caroliniana* and *lanceolata.* Types of a more recent origin may be *asarifolia* and *Sibirica* passing into the annual species of *Limnia.* As *desciscentes* we have placed *Naiocrene* and *Alsinastrum*, and parallel with these *Montiastrum.* In this classification the large-rooted species with monopodial shoots, and with both fore-leaves developed precede the slender-rooted *asarifolia* and *Sibirica* with perennial rhizomes, monopodial shoots, and distinct fore-leaves; then follow the annual species of *Limnia* of otherwise the same structure. Deviating from these is the bulbiferous *Naiocrene* with monopodial shoot, but with the fore-leaves merely rudimentary; furthermore the stoloniferous *Alsinastrum* with the fore-leaves of very unequal size, and with the shoot terminated by an inflorescence, similar to *Montiastrum*, but in this only one fore-leaf is developed in the shape of a small sheath.

EXPLANATION OF PLATES

Plate I.

Fig. 1. *Claytonia megarrhiza* PARRY; natural size.
— 2. An inflorescence.
— 3, 4 and 5. Leaves, showing variation in outline.
— 6. The calyx.
— 7. The corolla laid open showing the stamens.
— 8. The pistil.
— 9—14. The capsule, showing various stages of the opening.
— 15. The seed.

Figs. 2—5 are drawn in natural size; figs. 6—15 are magnified.



Autor ad nat. delin.

Axel E. Aamodt Kjøbenhavn.

Plate II.

Fig. 1. Seedling of *Claytonia Virginica* L., showing the single cotyledon, and the long, primary root, swollen at the base.
— 2. *Claytonia sarmentosa* Mey.
— 3. *Claytonia Chamissonis* Esch.
— 4. *Claytonia parvifolia* Moc.

Figs. 1—4 are drawn in natural size.

Autor ad nat. delin.

Axel E Aamodt Kjøbenhavn.

Plate III.

Fig. 1. Seedling of *Claytonia megarrhiza* Parry.
— 2. *Claytonia Sibirica* L.
— 3. *Claytonia diffusa* Nutt.
— 4. *Claytonia linearis* Dougl.

Figs. 1—4 are drawn in natural size.

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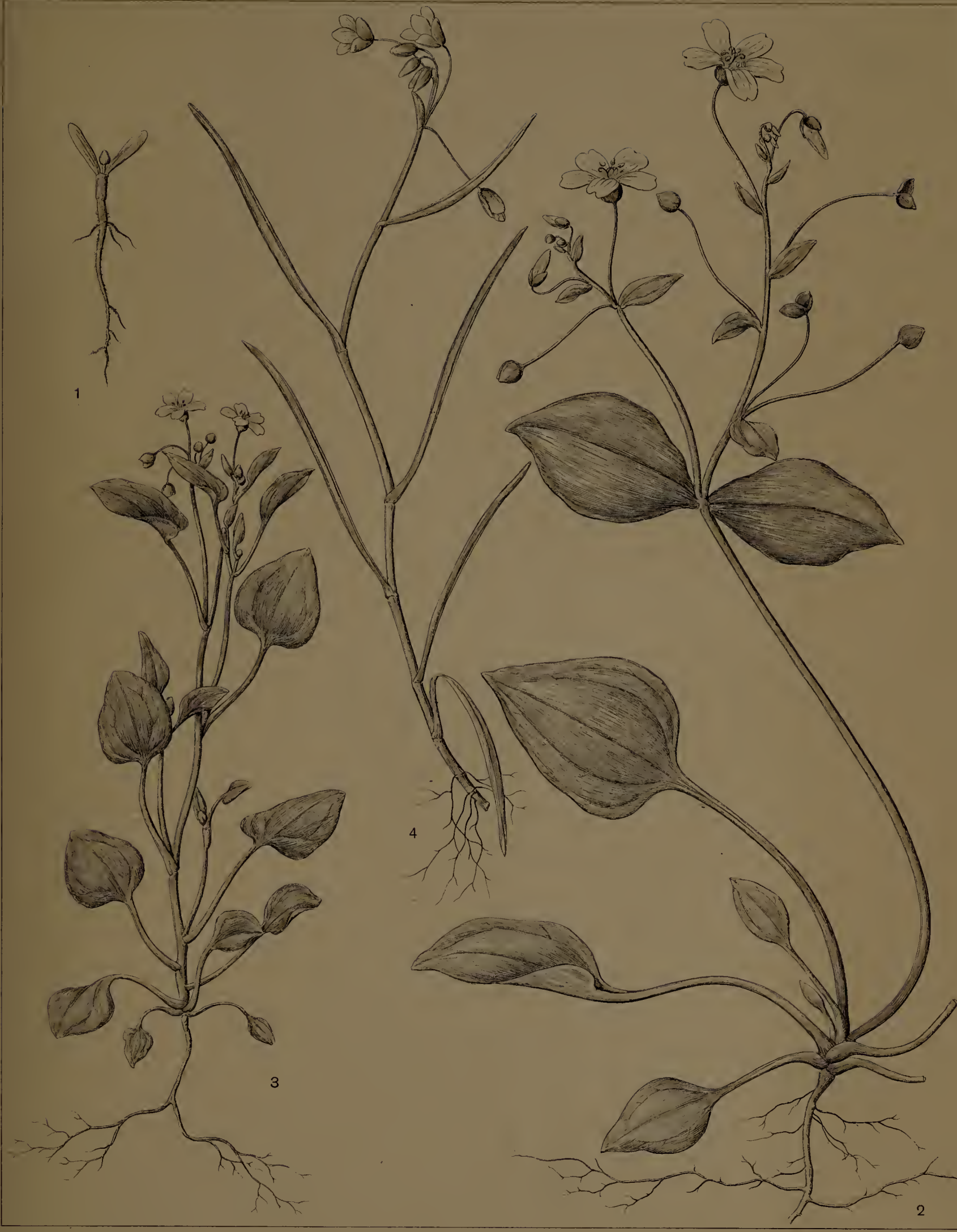

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